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EXPERIMENTAL STUDIES OF SPECIES-SPECIFICITY IN *CECROPIA*–ANT RELATIONSHIPS

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Abstract. Strict coevolution requires that interactions among organisms be species-specific. We assessed the relative roles of host- and habitat-specificity in determining the match between a genus of myrmecophytic trees and a guild of obligate plant-ants in the moist tropical forests of Madre de Dios, Peru. Four locally coexisting but habitat-restricted *Cecropia* species were cultivated in screen tents until all plants had developed myrmecophytic traits. Saplings were then placed within replicate blocks of each of two habitat types: riversides and small forest light gaps. Colonization events were recorded every 3 d between June and August of 1992, and queens were later removed from stem internodes for identification and brood censuses. A similar experiment, conducted in September through November of 1993, included just two species of *Cecropia* hosts. Effects of host species and habitat on queen colonization rates were evaluated by log-likelihood goodness-of-fit tests and contingency table tests. For three ant species, we also conducted queen preference experiments to compare queen behaviors across a range of host plants.

Differences among ants in the extent of habitat-specificity vs. host-specificity provide evidence for multiple evolutionary routes to obligate association with *Cecropia.* Habitat-specificity exceeded host-specificity in *Azteca ovaticeps* (Dolichoderinae), for which queen preference experiments revealed no significant discrimination among hosts. This extreme riverside specialist is thought to have descended from generalist live-stem nesters in second-growth habitats. In *Azteca australis,* host-specificity was strong, and in this species only, directed toward hosts where brood production was most successful. Conflicting habitat associations in the two experiments indicated the weakness or absence of a consistent habitat affiliation in *Azteca australis* and suggested that colonization frequencies were influenced instead by proximity to foundress sources. Close relatives of *A. australis* live in exposed carton nests, which may have been positioned ancestrally on key resource plants, e.g., those producing lipid- and amino-acid-rich pearl bodies. *Pachycondyla luteola* (Ponerinae) exhibited both strong habitat and host associations and may have undergone pairwise coevolution with its forest-gap-dwelling primary host. Queens of *Camponotus balzani* (Formicinae), possibly a recent and secondary associate of *Cecropia,* were overrepresented in forest gap habitat but were host generalists, underrepresented only on a host with extremely small internodes. Apparently greater host-specificity in *C. balzani* at later stages of colony establishment may be due to differential post colonization mortality on the various hosts.

Attack of ant queens by parasitoid wasps was strongly concentrated in the linear riverside habitat and weak to absent in the patchily distributed forest gap habitat. Due to lower rates of either parasitoid attack or other forms of queen mortality, *Camponotus balzani* experienced greater success in the forest gap habitat, where it was overrepresented in colonization experiments.

Historical coincidences and preadaptations appear to have strongly influenced pairings between *Cecropia* species and their obligate plant-ants and account for much of the "apparent" niche partitioning observed in the system. Species-specificity seems to be determined mainly by coincident habitat affiliations of ants and plants ("coordinated dispersal") and by preadapted capacities of ants to distinguish among host-plant species. Multiple mechanisms for species-specificity may be characteristic of relationships in which associates disperse separately from one another (i.e., show horizontal transmission). Our results are consistent with the view that coadaptation and co-cladogenesis are more likely in systems where dispersal of associates is tightly coupled.

Key words: *ant-plant; ants;* Cecropia; *coevolution; colonization; coordinated dispersal; ecological fitting; habitat-specificity; host-specificity; mutualism; parasitoid wasps; preadaptation.*

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Introduction

A key challenge of coevolutionary studies is to understand the ecological and evolutionary factors driving interacting species to undergo progressive bouts of reciprocal evolutionary change (Ehrlich and Raven 1964, Janzen 1980, Thompson 1989). One approach to this challenge is to study the ecological conditions promoting or impeding species-specificity in associations of two interacting guilds of species (Thompson 1994). Pairwise specificity is a prerequisite for coevolution sensu stricto (Janzen 1980). Conversely, lack of specificity should lead to either diffuse coevolution (possibly as qualified by Thompson 1994) or to the dissolution of interactions.

We studied the determinants of species-specificity in relationships between a group of myrmecophytic trees (ant-plants, or plants regularly housing ant colonies) and their obligate ant inhabitants. Many plants worldwide have evolved mechanisms for attracting ants that defend against herbivory and, in some cases, against encroaching vines (reviewed in Beattie 1985, Benson 1985, Huxley 1986, Davidson and McKey 1993). In a subset (all tropical) of these relationships, ant colonies live inside host stems or domatia for the entire colony life history, and the associations are obligate (or approximately so) for one or both partners (reviewed in Davidson and McKey 1993). Although both lifelong association and the absolute requirement for a partner are thought to favor species-specificity (Schemske 1983), a number of both obligate myrmecophytes and plant-ants are known to have multiple associates (Wheeler 1942, Benson 1985, Huxley 1986, Ward 1991, Davidson and McKey 1993). In the majority of cases for which the origins of such multiple associates can be discerned, they have arisen by repeated de novo colonization or lineage switching over evolutionary time, rather than through co-cladogenesis of two interacting lineages (Davidson and McKey 1993).

Here we investigate the factors promoting species-specificity in relationships between myrmecophytic Peruvian *Cecropia* species (Urticaceae, Judd et al. 1994) and a group of ants obligately associated with these host trees. The availability of multiple, sympatric species of both partners (Davidson et al. 1991), and their ease of manipulation, make this an excellent experimental system. Because of the evolutionary importance of the colonization process in generating new partners and partnerships in diffusely coevolving guilds of ants and plants, we focus on the earliest stages of colonization of *Cecropia* saplings by four distantly related taxa of obligate plant-ants.

Cecropia biology and focal species

Cecropia is a genus of 60–70 species of mostly myrmecophytic pioneer trees (C. C. Berg, *personal communication*) associated with a variety of resident ant species (Longino 1989*b*, 1991*a*, *b*, Davidson et al. 1991, Davidson and McKey 1993). At least 11 *Cecropia* species occur in the tropical moist forests of the Department of Madre de Dios in southeastern Peru. Three of these species are uncommon, and one species (*C. sciadophylla*) forms only facultative associations with ants having generalized nesting habitats.

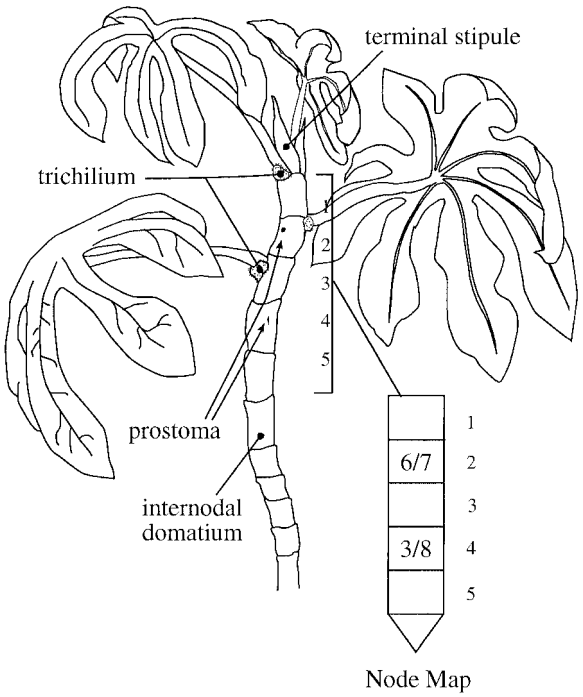

FIG. 1. Schematic drawing of a *Cecropia* sapling used in the colonization experiments. A pot label was used to record the dates of colonization in each internode.

The remaining seven myrmecophytic *Cecropia* have a similar biology. Ant-associated traits appear at a species-specific stage of sapling development, when stems expand and become hollow (Fig. 1), (Davidson and Fisher 1991, Folgarait and Davidson 1994). Thereafter, each hollow internode develops a small area of thin, unvascularized tissue called a prostoma. Ant queens colonize *Cecropia* by chewing a hole through a prostoma, entering the internode, and (with one exception) plugging the hole with parenchyma scraped from the internal stem walls. (Holes made elsewhere on the stem rupture phloem tubes and lead to the rapid filling of internodes with mucilaginous sap, a general feature of the Urticales.) Also, at a species-specific stage before, during, or after stem swelling, the base of each subsequent leaf petiole develops a trichilium, a pad of dense trichomes on which 1–2 mm long, glycogen-rich food rewards known as Müllerian bodies are produced (Rickson 1971). Inside the internode, a queen lays eggs and raises workers that eventually reopen and emerge from the prostoma to harvest both Müllerian bodies

from trichilia and lipid-rich pearl bodies from the lower leaf laminae.

Fused to adjacent internodes, each individual internode is a spatially separate unit, lined with tough sclerenchyma, accommodating single foundresses and their incipient colonies, or occasionally, multiple (pleometrotic) queens and their brood. Although most *Cecropia* saplings are colonized by multiple foundresses in different internodes, a single colony eventually dominates the entire sapling (Davidson et al. 1989, 1991, Longino 1989*a*, Perlman 1992). The mechanism of colony elimination is poorly understood, but success appears strongly related to early production of workers (Perlman 1992), and therefore, to early queen arrival.

Our studies focus on five of the seven myrmecophytic *Cecropia* species common in lowland Madre de Dios: *C. membranacea* Trecul, *C.* prov. *pungara* (in earlier work, *C.* prov. *tessmannii* [Davidson and Fisher 1991], or *Cecropia* sp. B [Folgarait and Davidson 1994, 1995]), *C.* prov. *puberula, C.* cf. *engleriana,* and *Cecropia* sp. A. (The majority of these species are probably undescribed. Provisional names were provided by C. C. Berg, who is nearing completion of a monograph on the genus. See *Acknowledgments* for information on voucher collections of these species.) Phylogenetic analyses of morphological data identify *C. membranacea* and *C.* prov. *pungara,* and *C.* cf. *engleriana* and *C.* sp. A as two pairs of sister species (D. Davidson, *unpublished data*). Although molecular sequence data from the hypervariable ITS I and II regions of nuclear ribosomal DNA confirm the close association of *C. membranacea* and *C.* prov. *pungara,* the consensus tree leaves the relationship between *C.* cf. *engleriana* and *C.* sp. A unresolved (D. W. Davidson, *unpublished data*). *Cecropia* prov. *puberula* was not included in these analyses, but our finding of occasional sapling hybrids between this species and *C.* prov. *pungara* suggests that the affinities of *C.* prov. *puberula* may lie near *C.* prov. *pungara.* We inferred hybrid status from three pieces of evidence: (a) the putative hybrids were morphologically intermediate between saplings of *C.* prov. *pungara* and *C.* prov. *puberula*; (b) the two species flower at the same time of year in the same habitat (D. W. Yu and D. W. Davidson, *unpublished data*); and (c) the putative hybrids were sprouted from a tiny percentage of seeds collected from adults of *C.* prov. *pungara* and are thus unlikely to be an undetermined species.

Site characteristics and habitat associations of Cecropia

At lower elevations in Madre de Dios, the vegetation is classified as moist-to-seasonal tropical forest (annual rainfall ≈2100 mm). Habitat is continually reworked by the meander loops of rivers that leave a closely packed, small-scale mosaic of soil types of differing ages and fertilities (extensive reviews in Terborgh 1983, Foster et al. 1986, Salo et al. 1986, Foster 1990, Gentry 1990). The constant river meandering creates thousands of kilometers of beaches, exposed cliffs and riverbanks, here referred to collectively as riverside habitat. Depending on their species-specific habitat affiliations, *Cecropia* establish in riverside habitat and streamsides, or in small-to-large treefall gaps within mature forest (Davidson et al. 1991).

Cecropia species differ in their frequencies on successional river beaches (successional forests), on young and fertile soils within the contemporary river floodplain (mature lowland "high ground" forests) and on relatively old and nutrient-poor soils (mature upland forests), generally <50 m above adjacent lowlands (D. W. Yu and D. W. Davidson, *unpublished data*). Unlike the successional forests of Madre de Dios and the varzeas and igapos of the Brazilian Amazon, mature lowland forests in the Peruvian Amazon are not seasonally flooded.

Closely related *Cecropia* species inhabit markedly different light environments (Davidson and Fisher 1991). *C. membranacea* establishes almost exclusively on open and sunny river beaches, while *C.* prov. *pungara* lives in seasonally flooded soils in small-to-large treefall gaps in lowland forests and under closed canopies at the edges of seasonal swamps (*Ficus trigona* and *Mauritius* swamps). *C.* cf. *engleriana* occupies relatively large treefall gaps along streams and gullies in upland forest and, occasionally, large treefall gaps, streamsides, and successional river beaches in lowland forest, but *C.* sp. A occurs primarily in small forest gaps in the upland forests. *C.* prov. *puberula* establishes principally in light gaps within lowland forests. Species-specific habitat associations allow the five focal *Cecropia* species to be grouped (cutting across phylogenetic lines) as either "pioneers" resident in riverside or streamside habitat (*C. membranacea* and *C.* cf. *engleriana*), or forest "gap species" (*C.* prov. *pungara, C.* sp. A, and *C.* prov. *puberula*) (Table 1).

Ant associates of Cecropia

In Madre de Dios, five ant species produce persistent colonies exclusively in myrmecophytic *Cecropia,* and are therefore considered to be *Cecropia* specialists (Davidson and Fisher 1991). These ants include sister species *Azteca ovaticeps* Forel and *Azteca alfari* Emery (subfamily Dolichoderinae, Longino 1991*b*), as well as *Azteca australis* Wheeler, *Camponotus balzani* Emery (Formicinae) and *Pachycondyla luteola* Roger (Ponerinae). The taxonomic diversity represented in these obligate associates of *Cecropia* is typical of that seen in other ant–myrmecophyte systems (Davidson and McKey 1993) and arises mainly from repeated evolutionary colonizations of *Cecropia* by unrelated ant lineages. Only in sister species *A. ovaticeps* and *A. alfari* are relationships with *Cecropia* likely due to descent from a common ancestor associated with *Cecropia. A. australis* belongs to a different clade within *Azteca,* and its association with *Cecropia* appears to

TABLE 1. Census of mature *Cecropia* trees in the Tambopata–Candamo Reserve Zone, Manu National Park and Cuzco Amazonico (all in Madre de Dios, Peru; adapted from Davidson and Fisher 1991). *Cecropia* species are sorted by habitat association. Sample sizes reflect the natural densities of these trees, except that continuous *Cecropia* stands along major rivers are underrepresented, relative to populations along major tributary streams (also riverside habitat) and forest gap habitat. (These stands contained mainly *A. ovaticeps/alfari* in *C. membranacea.*) Percentages indicate the proportion of each host species occupied by each ant species. The dominant ant species in each *Cecropia* species is underlined.

			Ant species (%)			
Habitat	*Cecropia* species	*n*	*Camponotus balzani*	*Azteca ovat./alfari*	*Aztec australis*	*Pachycondyla luteola*
Riverside	*membranacea*	53	30	49	21	...
	cf. *engleriana*	6	...	83	17	...
	polystachya	7	14	57	29	...
Forest gap	prov. *pungara*	31	10	...	...	90
	sp. A	17	...	...	100	...
	prov. *puberula*	17	...	...	100	...
	ficifolia	24	52	...	48	...

be independently derived (Longino 1991*a*, *b*, Ayala et al. 1996).

Relationships between ants and Cecropia

A census of adult *Cecropia* trees in the Manu National Park and the Tambopata Reserve Zone (both in Madre de Dios) reveals a decidedly nonrandom pattern of association between ant species and *Cecropia* species (Table 1, adapted from Davidson and Fisher 1991). Relationships range from highly species-specific (*Pachycondyla luteola* on *C.* prov. *pungara*) to somewhat specific (*Azteca ovaticeps* on all three pioneer species, but none of the related gap species), to even more general associations (those involving *Camponotus balzani* and *A. australis*).

What factors determine the disparate host ranges of these four ant species? Natural selection acting to increase the fitnesses of ants and/or plants may favor particular combinations of ant and plant species. Although all myrmecophytic *Cecropia* species provide both food and nest sites for ants, interspecific variation in rates of food body production and stem elongation (Folgarait and Davidson 1994) might influence the rates at which colonies can grow and reproduce, and the various ant species may proffer different degrees of protection against herbivores and competitors of their hosts (Davidson and Fisher 1991). Alternatively, matches between symbiotic ants and plants might be determined mainly by "ecological fitting" (sensu Janzen 1985), for example, by the ancestral habitat associations of both plants and ants.

Here we describe experiments to discriminate the relative importance of host- and habitat-specificity in determining the patterns of association between *Cecropia* species and their ants. By placing focal host species with different habitat associations into both riverside and gap habitats, and then recording colonization frequencies for the various ants, our experiments are designed to disentangle the confounding effects of habitat-specificity and host-specificity on species pairings (Table 1). The same experiments should also indicate the extent to which observed patterns of species association in natural communities can be accounted for by factors acting prior to or at colonization rather than after colonization. Finally, whether ants exhibit either habitat-specificity, host-specificity, or both, we attempt to determine whether the typical hosts or habitats of these ant species are those in which the ants do best during the earliest stages of colonization.

METHODS

Study site

Our experiments were carried out within the trail system of the Tambopata Jungle Lodge (69° 22′ W, 12° 50′ S; 400 m elevation), an ecotourism lodge lying ≈60 km upstream from the town of Puerto Maldonado on the Tambopata River (Fig. 2). The lodge and river lie within the 1.5×10^6 ha Tambopata-Candamo Reserve Zone in the Department of Madre de Dios.

Colonization experiment one (CE1)

We conducted two colonization experiments, one in 1992 and another in 1993. Each experiment was designed to separate evidence for host-specificity and habitat-specificity in *Cecropia*-ants by placing both forest gap and pioneer *Cecropia* in common gardens in both forest gap and riverside habitats. As hosts in colonization experiment 1 (CE1), we used two pioneer species (*C. membranacea,* and *C.* cf. *engleriana*) and two forest gap species (*C.* prov. *pungara* and *C.* prov. *puberula*). All except *C.* prov. *puberula* establish naturally within the study area, and *C.* prov. *puberula* is found commonly nearby). Seedlings of the four *Cecropia* species were cultivated from seeds germinated in petri dishes, and transferred to progressively larger soil bags containing a 50:50 mixture of local sand and soil. Saplings in 20-L soil bags were cultivated in screen tents until they had swollen stems, prostomata, trichilia, and leaf morphologies typical of the developmental stage at which ants colonize.

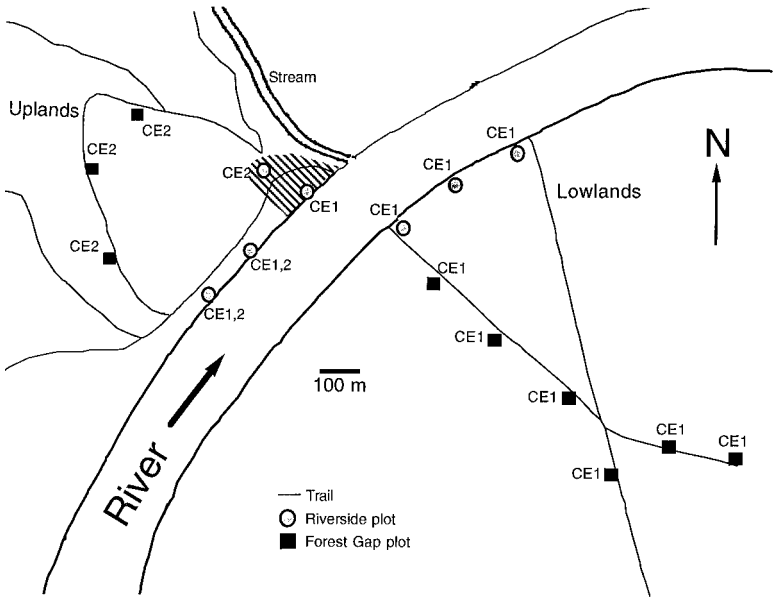

FIG. 2. Map of the Tambopata Jungle Lodge research area, showing the locations of the plots used in both colonization experiments. The diagonally shaded area indicates the lodge clearing. The map is drawn roughly to scale.

On 28 May 1992, we placed five individuals of each *Cecropia* species into each of 12 plots, for a total of 60 plants per species. Plants were placed at random in a 4 × 5 point grid, with individual saplings spaced 2 m apart within 8 × 8 m blocks. Six blocks were located along a 1.3-km transect in lowland, floodplain forest, and were spaced on average 250 m apart in forest gaps that we created or augmented. The other six blocks were located in riverside habitat along the banks of the Tambopata River. Three of the blocks were spaced evenly on a 450-m transect along the beach side of a river meander loop. Three others were placed across the river, 100 m upstream along an exposed cliff, and were evenly spaced along a 400-m transect (Fig. 2). Our design thus includes three treatments: habitat (riverside vs. gap), host plant species (four levels), and block within habitat (six levels) (Fig. 2). Each plant had at least three, and often more than five internodes available for colonization by different queens. With the possible exception of *C.* prov. *pungara* (see *Results by ant species*: *Pachycondyla luteola*), uncolonized internodes were available continuously throughout the experiment.

We checked each plant every 3 d for evidence of ant colonization through the prostomata. We noted the date and position of each colonization event on a map of the plant (Fig. 1), and left the queens in their internodes until the end of the experiment (late July). To preclude the emergence of incipient colonies, whose workers might have killed unrelated queens and colonies, we waited just 2 mo before collecting all queens from all plants. We scored the presence or absence of brood for each live queen and registered the presence or absence of the larvae and pupae of parasitoid wasps in internodes with dead queens. Multiple dead queens in a single internode were counted by the number of heads present. Finally, for each colonization event detected, we calculated the number of days between the date of observed colonization and the date of collection.

In most cases, we had no difficulty distinguishing ant species. Even dead queens of *A. australis, C. balzani,* and *P. luteola* could be identified reliably by their head shapes and colors. However, the two closely related *Azteca* species, *A. ovaticeps* and *A. alfari,* differ morphologically in only a few subtle traits and could not be identified reliably to species when dead and partially decomposed. Therefore, we pooled all *A. ovaticeps* and *A. alfari* together in our analyses. Since *A. ovaticeps* is far more common than *A. alfari* in this region (probably <1 *A. alfari* to 20 *A. ovaticeps* queens; identifications by J. T. Longino [1989*b*]), the colonization results mainly reflect the habitat and host associations of *A. ovaticeps.* In fact, all of the *A. ovaticeps/alfari* queens collected for the Queen Preference experiment (see *Results by ant species*: *A. ovaticeps/alfari*) were *A. ovaticeps.*

Since ants can be extracted from *Cecropia* without damaging unoccupied, adjacent internodes, we were able to collect another group of queens from these same hosts 4 wk later on 31 August. Because the results of the two collections were similar, we pooled the data in our analyses. All four ant species produce ălates (winged reproductive males and females) throughout the year (D. W. Yu and D. W. Davidson, *personal observations*), and colonization by the four species took place throughout both experimental runs.

The effects of habitat and host species on colonization rates were assessed directly for each ant species

from the colonization records. Rates of queen mortality and brood production provide estimates of success as influenced by host and habitat and were used to determine whether success was greater in typical than atypical hosts and habitats.

Colonization experiment 2 (CE2)

A second colonization experiment was conducted from June to November of 1993, this time as part of a larger field experiment. We used closely related hosts, *C.* cf. *engleriana* (a pioneer) and *Cecropia* sp. A (a gap species). Seedlings of both species were cultivated from seed and, when 5 cm tall, were planted in the soil within six 8 × 8 m plots located in upland forest, where both species establish naturally (D. Yu, *personal observation*). In each plot, 40 plants, 20 of each species, were placed at randomly chosen points in a 6 × 7 point grid with two vacant points. Three plots were in forest gaps, more or less equally spaced along an 800-m transect. Two plots were located along a 400-m transect near the river on an exposed cliff. The final plot lay 250 m from the river in a large, human-made clearing, open all the way to the river and near a stream (Fig. 2). Based on earlier surveys of *Cecropia*-ants in such clearings (e.g., Davidson and Fisher 1991, and confirmed in *Results* below), this plot was treated as a riverside plot. Our analyses thus consider three treatments: habitat (riverside vs. forest gaps), host species (*C.* sp. A and *C.* cf. *engleriana*), and three blocks within each habitat.

Transplanted to the field in June, most plants had developed myrmecophytic traits by the end of September. Beginning in late August and ending in late November, colonizations were recorded for each plant, as in CE1. Thirteen weeks after our colonization records began, all queens were removed from internodes, and identified and recorded as in CE1. CE2 differed from CE1 in that plants were transplanted to the field earlier in seedling development and prior to the onset of myrmecophytism. In the higher light, riverside plots, *C.* cf. *engleriana* grew larger than did *Cecropia* sp. A, but this difference was less pronounced at the lower light levels characteristic of forest gap habitat (D. W. Yu and D. W. Davidson, *unpublished data,* see also Folgarait and Davidson 1994).

Queen preference experiment (QP)

Foundresses could fail to colonize a host species not only because queens rank certain host species below others, but also because of differences in plant apparency (e.g., due to disparities in plant size), or in a queen's ability to penetrate the prostoma. To better define queen responses to particular host species, we carried out a behavioral experiment in 1992, with three of the obligate *Cecropia*-ants: *Azteca ovaticeps, Azteca australis,* and *Pachycondyla luteola,* whose queens appear to return to normal behavior after handling. *Camponotus balzani* queens were not tested because they flee after handling.

Five uncolonized saplings of each of four host species, *C. membranacea, C.* prov. *pungara, C. puberula,* and *C.* cf. *engleriana,* were drawn haphazardly from the sapling pool used in CE1. Individual ant queens collected from various species of wild and cultivated saplings (the latter set out by us) were placed sequentially on representatives of the four *Cecropia* species; each queen's behavior was then monitored over a 60-min period on each host species. Between trials, queens were held in plastic containers for at least 20 min. The order of plant species (*membranacea, engleriana, puberula, pungara*) was varied among queens so that, cumulatively, every plant species was presented in each rank (first to fourth) five times for each ant species. In total, trials included 20 queens of each ant species.

Queens were introduced at the terminal stipule. In most cases, they ran upward, paused at the top of the plant, and then began one of the following behaviors, which we have classified into six categories.

0) Did nothing for 60 min.
1) Left the plant within the first 2 min.
2) Left the plant after 2 min and before 60 min.
3) Tried but failed to colonize within 60 min (scored for queens that exhibited the stereotyped behaviors normally leading to colonization but were unable to enter a prostoma; rapid antennation of the plant surface and chewing on various plant parts).
4) Colonized the plant (scored for queens that were able to create an entrance hole in a prostoma).
5) Walked on the plant for 60 min.

Any queen leaving the plant for the first time within the first 30 s was considered disturbed and placed back on the plant for a second trial. For purposes of analysis, behaviors 0, 1, 2, and 5 were pooled and counted as instances of the ant rejecting the plant. Behavior 3 occurred mainly with one ant–*Cecropia* combination, *A. australis* and *C.* prov. *pungara.* Behavior 4 was scored as a colonization event.

We modified the above protocol for *P. luteola* queens, which during CE1, often stood for weeks on the external stems of *C. membranacea, C.* prov. *pungara,* and *C.* prov. *puberula* before colonizing these saplings. Since *P. luteola* foundresses were never noted on or in *C.* cf. *engleriana* saplings in the colonization experiments, we compared *C.* cf. *engleriana* with *C.* prov. *pungara,* the typical host plant, and the species most likely to elicit colonizing behavior within the allotted time. Our purpose was to test whether *P. luteola* actively rejects *C.* cf. *engleriana,* or whether its absence from this host in colonization experiments must be attributable to some other factor, e.g., the absence of some attractant cue by which these queens locate their hosts from a distance.

The behavioral assays were conducted during midday (1000 to 1400) in a screen tent placed in the middle

TABLE 2. Colonization frequencies from CE1. Counts represent numbers of queens totalled over both collection periods (see text) and are subtotalled by host species and habitat. See *Results* and Table 8 for details of censuses and significance tests.

		Ant species											
		Camponotus balzani			*Azteca ovaticeps/alfari*			*Azteca australis*			*Pachycondyla luteola*		
Habitat	*Cecropia* species	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total
Riverside	cf. *engleriana*	...	...	...	8	6	14	22	20	42	...	...	...
	membranacea	2	3	5	15	10	25	4	5	9	4	...	4
	prov. *puberula*	...	1	1	4	2	6	26	18	44	...	...	...
	prov. *pungara*	1	...	1	1	1	2	3	2	5	18	2	20
	Total	3	4	7	28	19	47	55	45	100	22	2	24
Forest gap	cf. *engleriana*	8	1	9	...	...	...	14	5	19	...	...	...
	membranacea	9	...	9	...	...	...	2	...	2	26	2	28
	prov. *puberula*	5	...	5	...	...	...	28	2	30	4	...	4
	prov. *pungara*	7	...	7	...	...	...	...	...	...	80	2	82
	Total	29	1	30	...	...	...	44	7	51	110	4	114

of an open field. Preliminary assays at other hours of the day, or in the shade, failed to elicit colonizing behavior in most foundresses. Most queens colonizing *Cecropia* in the wild also do so during midday (D. W. Yu and D. W. Davidson, *personal observations*). Higher ambient temperatures and reduced activity of avian predators may account for higher queen activity at this time.

Statistical analyses

Frequencies of queen colonization, mortality, and brood production were analyzed using log-likelihood ratio goodness-of-fit tests (G tests adjusted with the William's correction and reported as G_{adj}, Sokal and Rohlf 1995) or log-likelihood contingency table tests (reported as G [Systat 1992]), as described below. Monte Carlo contingency table tests (25 000 trials, Engels 1988*b*) were substituted for log-likelihood contingency table tests when expected frequencies were below five, unless the log-likelihood contingency table test was not significant. Post hoc comparisons of host associations were made using log-likelihood ratio goodness-of-fit tests and values adjusted with the William's correction. Post hoc tests were judged for significance conservatively after multiplying the P values by the total number of pairwise comparisons possible (e.g., by factor of seven, given four hosts). Original P values are reported.

Because testing one queen on multiple hosts does not constitute multiple independent tests, results of the QP experiment were analyzed using McNemar's tests (rather than contingency table tests), which correct for the nonindependence of multiple tests on the same subject (Sokal and Rohlf 1995). For each ant species, we tested the a priori hypothesis that queens would preferentially colonize or attempt to colonize (behaviors 4 and 3 vs. behaviors 0, 1, 2, and 5) the host species or species pair which was colonized significantly more often in CE1. Details of the post hoc tests are given in the *Results* section. Exact binomial P values were calculated using Engels (1988*a*).

RESULTS

Tests of block effects and interactions among treatments

Before considering the responses of each of the ant species independently, we summarize colonization results and analyze the effects of treatment interactions and block on frequencies of colonization and queen mortality, and on brood production. We also analyze the distribution of parasitoid wasps, which were found to kill colonizing queens of several ant species.

Colonization frequencies.—We collected a total of 373 and 484 colonizing queens of the obligate *Cecropia*-ants in CE1 and CE2, respectively (Tables 2 and 3). Also collected were two queenright colonies (i.e., colonies with queens) of *Crematogaster* sp. (CE1), one colony of *Pachycondyla unidentata* (CE1), and one queen of *Pseudomyrmex gracilis* Fabricus (CE2). These species are not obligate *Cecropia* ants and will not be considered further. Vouchers of all ant species are deposited in the Museum of Comparative Zoology at Harvard.

Lumping live and dead queens, we analyzed colonization frequencies for ant species across habitats and hosts. In both CE1 and CE2, the interaction effects of habitat and host species on colonization frequencies of *A. australis, C. balzani,* and *P. luteola* were not significant ($P > 0.05$). Only two *A. ovaticeps/alfari* queens colonized the forest gap habitat (CE2 only), so these species were not tested for habitat by host interaction effects. Based on the nonsignificant interaction effects, we analyzed the effects of habitat and plant species separately.

With two exceptions, block effects on colonization frequencies across host species within habitats were not significant ($P > 0.05$, see *Methods*). Exceptions were *A. australis* in forest gap habitat in CE1 (Monte

TABLE 3. Colonization frequencies from CE2. Counts represent numbers of queens collected, and are subtotalled by host species and habitat. See *Results* and Table 8 for details of censuses and significance tests.

		Ant species								
		Camponotus balzani			*Azteca ovaticeps/alfari*			*Azteca australis*		
Habitat	*Cecropia* species	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total
Riverside	cf. *engleriana*	8	7	15	10	60	70	18	60	78
	sp. A	1	2	3	5	25	30	13	18	31
	Total	9	9	18	15	85	100	31	78	109
Forest gap	cf. *engleriana*	47	11	58	2	...	2	71	52	123
	sp. A	22	4	26	...	...	...	32	16	48
	Total	69	15	84	2	...	2	103	68	171

Carlo, $P = 0.001 \pm 0.001$ SE) and *C. balzani* in the forest gap habitat in CE2 ($G = 27.620$, df = 2, $P < 0.0001$). We pooled blocks within habitat for all but the exceptional cases, which were analyzed using replicated goodness-of-fit tests (Sokal and Rohlf 1995).

Mortality.—For each ant species, we compared the effect of habitat by host interactions on queen mortality (the distributions of live vs. dead queens, Tables 2 and 6). Habitat by plant interaction effects were not significant for dead *A. australis, C. balzani,* or *P. luteola* ($P > 0.05$ in both CE1 and CE2), and all *A. ovaticeps/alfari* queens were found in the riverside habitat. We therefore analyzed mortality separately by habitat and host species. We also analyzed the effect of blocks within habitats on the distribution of dead vs. live queens. Block effect within habitat was not significant ($P > 0.05$) for any ant species in CE1 or CE2, so we pooled the data over all blocks.

Brood production.—In each experiment, queens of three species were sufficiently abundant to test for habitat by host species interactions on brood production (Table 4). In CE1, interaction effects were not significant for either *A. australis* or *P. luteola* ($P > 0.05$), and *A. ovaticeps/alfari* was absent from forest gap habitat. Habitat by host interactions were also not significant for *A. ovaticeps/alfari, A. australis,* or *C. balzani* in CE2 ($P > 0.05$). Therefore, habitat and plant species effects on brood production were analyzed separately in each experiment. The distribution of live queens with brood vs. live queens without brood was not significantly affected by block ($P > 0.05$), so blocks were pooled for further analyses.

In CE1, the proportion of queens with brood differed significantly among ant species (Table 4). However, since ant queens appear to delay egg production for a number of days after colonization, most likely due to a delay in mobilizing resources, an ant species may have appeared to have low rates of brood production because many colonizations occurred late in the experimental run. In order to correct conservatively for late colonizations, we defined a minimum occupation time for each ant species. Minimum occupation times are calculated for individual ant species as the shortest occupation time (from colonization to collection dates) for any queen collected with brood. After correction for minimum occupation time, we found no significant

TABLE 4. For each of four ant species, numbers of queens with brood (eggs, larvae, pupae, and/or workers) compared to numbers of live queens without brood, for CE1 and CE2 separately.

		Ant species			
Experiment	Queen status	*Camponotus balzani*	*Azteca ovaticeps/alfari*	*Azteca australis*	*Pachycondyla luteola*
CE1	Live with brood	2	5	47	67
	Live, no brood†	30	23	52	65
	Live, ≥MOT, no brood‡	6	7	41	65
CE2	Live with brood	31	12	82	
	Live, no brood§	47	5	52	
	Live, ≥MOT, no brood‖	20	2	22	

† CE1: Queens with brood vs. live queens without brood ($G = 33.923$, df = 3, $P < 0.001$).

‡ CE1: Queens with brood vs. live, brood-lacking queens present for the minimum occupation time (MOT) or more. CB, 13 d; AO, 16 d; AA, 4 d; PL, 1 d; see text for explanation ($G = 2.851$, df = 3, $P = 0.415$).

§ CE2: Queens with brood vs. live queens without brood ($G = 11.121$, df = 2, $P = 0.004$).

‖ CE2: Queens with brood vs. live, brood-lacking queens present for ≥ MOT. CB, 6 d; AO, 14 d; AA, 6 d ($G = 6.700$, df = 2, $P = 0.035$).

TABLE 5. Distributions of wasps and their ant hosts across habitats.

Experiment		Habitat: Forest gap	Habitat: Riverside
CE1†	*Conoaxima* sp.	0	19
	Ant queens‡	51	147
CE2§	*Conoaxima* sp.	12	25
	Ant queens‖	256	227

† CE1: Wasp distribution is significantly biased toward riverside habitat (Monte Carlo, $P = 0.005 \pm 0.000$ SE).

‡ *A. ovaticeps* and *A. australis*.

§ CE2: Wasp distribution is significantly biased toward riverside habitat ($G = 5.916$, df = 1, $P = 0.015$).

‖ *A. ovaticeps, A. australis,* and *C. balzani*.

differences among ant species in the proportions of queens with brood (Table 4). In contrast, in CE2, the proportion of queens producing brood was significantly lower in *C. balzani* than in the other two ant species. This result held both before and after correction for minimum occupation time (Table 4). Brood counts may have been biased downward and minimum occupation times upward in *Azteca ovaticeps/alfari* by the difficulty of detecting their extremely small eggs and early-instar larvae.

Parasitoid wasp distributions.—In CE1, 19 larvae, pupae, or adult parasitoid wasps of *Conoaxima* sp. (Eurytomidae, Chalcidoidea) were collected from dead *A. ovaticeps/alfari* and *A. australis* queens (Table 5), but were not noted in association with *Camponotus balzani* or *Pachycondyla luteola* queens. In CE2, a total of 37 larvae, pupae, and adults of the genus *Conoaxima* were found parasitizing queens of *C. balzani* and the *Azteca* species (Table 5). Wasps collected in both experiments were similar but cannot be identified reliably to species, because the parasitoids were collected mainly in immature form, and because the species-level taxonomy of *Conoaxima* remains poorly elucidated. Based on the recommendation of the expert on this genus, we consider it likely that all *Conoaxima* wasps collected are *C. aztecicida* (E. E. Grissell, *personal communication*). Vouchers have been deposited at the National Museum of Natural History (Smithsonian Institution).

In both CE1 and CE2, wasp distributions (summed over all ant species) were significantly more biased to the riverside habitat than were the distributions of their aggregate ant hosts (Table 5). However, within ant species and in both experiments, wasp distributions across plant species did not differ significantly from queen distributions over plant species (Tables 6 and 7), nor was parasitism by wasps associated disproportionately with any of the three ant hosts (CE1: riverside habitat, $G = 0.754$, df = 1, NS; CE2: riverside habitat, $G = 3.216$, df = 2, NS, and forest gap habitat, $G = 0.355$, df = 1, NS).

TABLE 7. Distributions of wasps and their ant hosts across *Cecropia* species, summed over both habitats in CE2.

Ant species		*Cecropia* species: cf. *engleriana*	*Cecropia* species: sp. A	Total
A. ovaticeps/alfari	*Conoaxima* sp.	6	3	9
	Ant queens	72	30	102
A. australis	*Conoaxima* sp.	18	2	20
	Ant queens	201	79	280
C. balzani	*Conoaxima* sp.	7	1	8
	Ant queens	73	29	102

Note: The distribution of wasps does not differ significantly from the distribution of either *Azteca* species or *Camponotus balzani* over plant species (*A. ovaticeps*: Monte Carlo, $P = 1.000 \pm 0.000$ SE; *A. australis*: $G = 3.683$, df = 1, $P = 0.055$ (marginally not significant); *C. balzani*: Monte Carlo, $P = 0.440 \pm 0.003$ SE), or all three ant species together ($G = 2.872$, df = 1, $P = 0.090$).

Results by ant species

We now consider the response of each ant species in turn, and ask whether colonization frequencies vary significantly across habitats or hosts. In cases where there was a significant host treatment effect, we performed a post hoc analysis to identify heavily colonized host species. We analyzed mortality and brood production similarly.

Camponotus balzani

Colonization frequencies.—*Camponotus balzani,* the rarest ant, was overrepresented in the forest gap habitat in both CE1 and CE2 (Tables 2, 3, and 8). Host affil-

TABLE 6. Distributions of wasps and their ant hosts across *Cecropia* species in riverside habitat of CE1.

Ant species		*Cecropia* species within river habitat: cf. *engleriana*	*membranacea*	prov. *puberula*	prov. *pungara*	Total
A. ovaticeps/alfari	*Conoaxima* sp.	2	6	0	0	8
	Ant queens	14	25	6	2	47
A. australis	*Conoaxima* sp.	6	1	4	0	11
	Ant queens	42	9	44	5	100

Note: The distribution of wasps over host species is not significantly different from distributions of either *Azteca* species independently (*A. ovaticeps/alfari*: $G = 3.103$, df = 3, $P = 0.376$; *A. australis*: $G = 1.520$, df = 3, $P = 0.678$), or both ant species together ($G = 3.882$, df = 3, $P = 0.274$).

TABLE 8. Summary results from CE1 and CE2: colonization frequencies and mortality by habitat and host species, including significance levels.

		Colonization frequencies					
		Habitat			*Cecropia* species		
Ant species	Expt.	More in	G_{adj}†	*P*	More in‡	G_{adj}§	*P*
C. balzani	CE1	Forest	15.194	<0.001	none	3.531	NS
	CE2	Forest	46.112	<0.001	E	8.497#	<0.005
A. ovaticeps/alfari	CE1	River	56.235	<0.001	E, M	27.030	<0.001
	CE2	River	121.120	<0.001	E	17.732	<0.001
A. australis	CE1	River	16.139	<0.001	E, Pb	51.159††	<0.001
	CE2	Forest	13.818	<0.001	E	54.884	<0.001
P. luteola	CE1	Forest	63.556	<0.001	Pg	188.866	<0.001

† *G* test for goodness of fit, extrinsic null hypothesis of equal distribution between habitats, df = 1.
‡ M = *C. membranacea,* Pg = *C.* prov. *pungara,* Pb = *C. puberula,* E = *C.* cf. *engleriana.* See *Results by ant species* for details on post hoc comparisons.
§ *G* test for goodness of fit, extrinsic null hypothesis of equal distribution among *Cecropia* species, CE1, df = 3; CE2, df = 1.
‖ Contingency table test, pooled over host species, df = 1.
¶ Contingency table test, pooled over habitats, CE1, df = 1; CE2, df = 3.
# Riverside habitat only. There is a significant block effect in the forest gap habitat, but in both habitats, *C.* cf. *engleriana* is colonized significantly more often. See *Results: Colonization frequencies* for details.
†† Riverside habitat only. There is a significant block effect in the forest gap habitat, but *Cecropia* species preferences are the same in both riverside and gap habitats. See *Results: Colonization frequencies* for details.

iation was not significant in CE1. However, during CE2, queens colonized *C.* cf. *engleriana* disproportionately in the riverside habitat, and in forest gap habitat, *C. balzani* colonized *C.* cf. *engleriana* disproportionately in block 1 (39 vs. 3 queens, *G* test for goodness-of-fit, extrinsic null hypothesis of equal distribution among plant species, $G_{adj} = 36.179$, df = 1, $P < 0.001$). Although plant species association was not significant in the other two blocks (block 2: 11 vs. 19 and block 3: 8 vs. 4 queens in *C.* cf. *engleriana* vs. *Cecropia* sp. A, respectively), the pooled data showed a significant association with *C.* cf. *engleriana,* compared to *C.* sp. A (58 vs. 26 queens, $G_{pooled} = 12.504$, df = 1, $P < 0.001$).

Mortality.—In both CE1 and CE2, the ratio of dead to live queens was significantly higher in the riverside habitat than in forest gaps (Tables 2, 3, and 8), but mortality did not vary significantly by host species (Table 8).

Brood production.—In CE1, *C. balzani* queens were too few to analyze the effects of habitat and host on brood production (Table 4). Across habitats and hosts in CE2, the distributions of queens with brood did not differ significantly from those of live brood-lacking queens present for at least the minimum occupation time (host species: Table 9; habitat: $G = 0.001$, df = 1, $P = 0.990$).

Azteca ovaticeps/alfari

Colonization frequencies.—All 47 queens of *A. ovaticeps/alfari* in CE1, and all but 2 of 100 queens in CE2, colonized *Cecropia* saplings in the riverside habitat (Tables 2, 3, and 8). In CE1, colonization rates varied significantly with host species (Tables 2 and 8), and post hoc analyses showed that the two pioneer species, *C. cf engleriana* and *C. membranacea,* were colonized significantly more often than were the two gap species, *C.* prov. *puberula* and *C.* prov. *pungara* (39 vs. 8 queens, extrinsic null hypothesis of equal distribution between plant species pairs, $G_{adj} = 22.036$, df = 1, $P < 0.001$) (Tables 2 and 8). The distribution of *A. ovaticeps/alfari* within pairs did not differ significantly from the extrinsic null hypothesis of equal distribution (pioneer species, $G_{adj} = 3.105$, df = 1, NS; gap species, $G_{adj} = 1.970$, df = 1, NS). In CE2, pioneer *C.* cf. *engleriana* was colonized at significantly higher frequency than was *Cecropia* sp. A, a forest gap species (Table 8).

Mortality.—Because only two queens were collected in the forest gap habitat (both in CE2), the effect of habitat on mortality was not tested. Mortality did not vary significantly across host species in either experiment (Tables 2, 3, and 8).

Brood production.—Brood production did not vary significantly across host species in either experiment (Tables 9 and 10).

QP experiment.—*A. ovaticeps* queens did not show a significant preference for the pair *C. membranacea* and *C.* cf. *engleriana* over the other two host species (Table 11A). The summary QP results (Table 12) suggested that *A. ovaticeps* queens preferred the host species pair *C. membranacea* and *C.* prov. *puberula,* but a post hoc test revealed this pattern also to be nonsignificant (Table 11B). Despite the stiff, erect, urticating hairs of *C.* prov. *pungara,* and the comparatively small size of the *A. ovaticeps* queens, 5 of 20 *A. ovaticeps* queens managed to enter the prostoma of *C.* prov. *pungara* (Table 12). Since all queens were collected from *C. membranacea* saplings volunteering on river beaches, the lack of evidence for host species preferences

TABLE 8. Continued.

Mortality					
Habitat			*Cecropia* species		
More in	G‖	P	More in	G¶	P
River	10.977	<0.001	none	3.073	NS
River	7.519	0.006	none	0.185	NS
...	...	...	none	0.239	NS
...	...	...	none	0.000	NS
River	16.033	<0.001	none	3.636	NS
River	27.646	<0.001	none	3.660	NS
...	...	...	...	...	...

suggests that source plant effects (effects of previous experience on host species choices) are insignificant. We also tested for the effect of presentation order per se on the probability of colonizing a test sapling and found no significant effects in a contingency table test (data available upon request).

Azteca australis

Colonization frequencies.—*A. australis* was the most common ant species in both experiments (Tables 2 and 3). Its habitat associations, though significant in both experiments, differed in the two experiments. *A. australis* was disproportionately abundant in the riverside habitat in CE1 but was overrepresented in the forest gap habitat in CE2 (Tables 2, 3, and 8). In CE2, this ant was also overrepresented on *C.* cf. *engleriana* (Tables 3 and 8). Within the riverside plots of CE1, the distribution of this ant species was not independent of host species (Tables 2 and 8), and a series of post hoc goodness-of-fit pairwise comparisons detected significant overrepresentation of this ant on *C.* cf. *engleriana* and *C.* prov. *puberula,* relative to its occurrence on *C. membranacea* and *C.* prov. *pungara* (86 vs. 14 queens, extrinsic null hypothesis of equal distribution between host species pairs, $G_{adj} = 57.350$, df = 1, $P < 0.001$). In contrast, within each of these host plant pairs, *A. australis* colonized host species at approximately equal frequencies (extrinsic null hypothesis of equal distribution between species of pairs, *C. membranacea* vs. *C.* prov. *pungara,* $G_{adj} = 1.119$, df = 1, NS; *C.* cf. *engleriana* vs. *C.* prov. *puberula,* $G_{adj} = 0.0462$, df = 1, NS).

In CE1, because block effects were significant for *A. australis* in the forest gap habitat, we analyzed host species associations using a replicated goodness-of-fit test. In order to conduct this test, zero values in each block were replaced with ones, making this a conservative test of host species associations. Colonization by *A. australis* queens was not statistically independent of host plant species in the gap habitat (extrinsic null hypothesis of equal distribution among plant species, $G_{pooled} = 27.548$, df = 3, $P < 0.001$, Tables 2 and 8). Post hoc comparisons revealed significant association with *C.* cf. *engleriana* and *C.* prov. *puberula,* relative to the pair of sister species, *C. membranacea* and *C.* prov. *pungara* (49 vs. 2 queens before adjusting for zeroes, and 49 vs. 7 queens afterwards, extrinsic null hypothesis of equal distribution between plant species pairs, $G_{pooled} = 35.434$, df = 1, $P < 0.001$). In contrast, within each of these plant pairs, *A. australis* colonized host species at approximately equivalent frequencies (extrinsic null hypothesis of equal distribution between plant species of a pair, *C.* cf. *engleriana* vs. *C.* prov. *puberula* [19 vs. 30 before adjustment for zeroes, and 19 vs. 32 afterwards], $G_{pooled} = 3.351$, df = 1, NS; only two colonizations in *C. membranacea* and none in *C.* prov. *pungara*). For all analyses, a lack of significance in $G_{heterogeneity}$ demonstrated that the observed block effect did not contribute to the significance of the host species effect.

Mortality.—In both CE1 and CE2, mortality was high (34 and 52%, respectively) and was significantly greater in the riverside habitat (Tables 2, 3, and 8). In CE1, mortality in the riverside habitat was high enough to negate the significantly greater colonization rate there (live queens only, 44 in forest gaps vs. 55 in riverside habitat, extrinsic null hypothesis of equal distribution between habitats, $G_{adj} = 1.219$, df = 1, NS). The distribution of dead vs. live queens did not differ significantly over the four *Cecropia* species in CE1 or CE2 (Tables 2, 3, and 8).

Brood production.—Brood production was significantly related to host species in CE1 (Table 10). Brood

TABLE 9. Distribution over host species of queens with and without brood in CE2.

Ant species	Queen status†	*Cecropia* species	
		cf. *engleriana*	sp. A
C. balzani‡	Live with brood	10	21
	Live, ≥ MOT, no brood	6	13
A. ovaticeps/alfari§	Live with brood	5	7
	Live, ≥ MOT, no brood	0	2
A. australis‖	Live with brood	28	54
	Live, ≥ MOT, no brood	8	14

† MOT = minimum occupation time. See *Results: Brood production* for explanation.
‡ *C. balzani* (contingency table test, $G = 0.002$, df = 3, $P = 0.960$).
§ *A. ovaticeps/alfari* (Monte Carlo, $P = 0.505 \pm 0.003$ SE).
‖ *A. australis* (contingency table test, $G = 0.037$, df = 3, $P = 0.847$).

TABLE 10. Distribution over host species of queens with and without brood in CE1. Numbers of *P. luteola* queens with larvae or pupae are noted separately in parentheses.

Ant species	Queen status†	*Cecropia* species			
		cf. *engleriana*	*membranacea*	prov. *puberula*	prov. *pungara*
A. ovaticeps/alfari‡	Live with brood	4	...	1	...
	Live, ≥ MOT, no brood	1	4	1	...
A. australis§	Live with brood	24	...	23	...
	Live, ≥ MOT, no brood	10	6	23	2
P. luteola‖	Live with brood	...	14 (0)	2 (0)	52 (14)
	Live, ≥ MOT, no brood	...	16	2	46

† MOT = minimum occupation time. See *Results: Brood production* for explanation.
‡ *A. ovaticeps/alfari* (Monte Carlo, omitting *C.* prov. *pungara*, $P = 0.071 \pm 0.002$ SE).
§ *A. australis* (Monte Carlo, using all four host species, $P = 0.001 \pm 0.000$ SE).
‖ *P. luteola* (using all queens and omitting *C.* cf. *engleriana*, $G = 0.380$, df = 2, $P = 0.827$); *P. luteola* (Monte Carlo, using only queens with larvae and pupae, $P = 0.036 \pm 0.001$ SE).

were produced only in *C.* cf. *engleriana* and *C.* prov. *puberula*. In CE2, brood were produced in both *C.* cf. *engleriana* and *Cecropia* sp. A, and the frequencies of brood production on the two hosts did not differ significantly (Table 9). In neither experiment did habitat significantly affect the proportion of queens with brood for live queens with resident times greater than or equal to the minimum occupation time (CE1, $G = 0.004$, df = 1, $P = 0.950$; CE2, $G = 0.000$, df = 1, $P = 0.988$).

QP experiment.—Consistent with the results from CE1 (Table 8), *A. australis* queens colonized or attempted to colonize *C.* cf. *engleriana* and *C.* prov. *puberula* significantly more often than they colonized or attempted to colonize *C. membranacea* and *C.* prov. *pungara* (Table 11C). A post hoc test revealed that queens did not differentiate between the first pair of hosts (Table 11D), and sample sizes were too small to test for host discrimination in the latter pair. Different factors accounted for the failure of *A. australis* queens to colonize *C. membranacea* and *C.* prov. *pungara*. On *C. membranacea*, failure was due principally to rejection of the host (19 of 20 cases), rather than to failure of attempts to enter the prostoma (1 of 20 cases) (Table 12). In contrast, on *C.* prov. *pungara*, 10 of 20 queens exhibited behaviors normally leading to colonization but were unable to colonize (Table 12). Queens walked rapidly over the plant surface, repeatedly antennated the stem, and chewed on various plant parts, including the terminal stipule, axillary buds, trichilia, and the stem wall. However, only one queen located the prostoma, and in that case, the stiff, erect, and urticating hairs prevented her from opening the stem at the prostoma. The same queens that failed to gain entry to *C.* prov. *pungara* colonized *C.* prov. *puberula* and/or *C.*

TABLE 11. Queen preference (QP) experiment analyzed using McNemar tests. A priori tests contrast overrepresented and underrepresented host species pairs from CE1 (Table 8).

(A) *A. ovaticeps* a priori†

Pb or Pg	E or M: +	E or M: −
+	10	1
−	3	6

$P = 0.375$

(B) *A. ovaticeps* post hoc

E or Pg	M or PB: +	M or PB: −
+	7	1
−	6	6

$P = 0.070$

(C) *A. australis* a priori

M or Pg	E or Pb: +	E or Pb: −
+	11	0
−	7	2

$P = 0.008$

(D) *A. australis* post hoc

E	Pb: +	Pb: −
+	12	4
−	2	2

$P = 0.453$

(E) *A. australis* post hoc

Pg	M: +	M: −
+	0	10
−	1	9

$P = 0.006$

(F) *P. luteola* a priori

E	Pg: +	Pg: −
+	0	0
−	18	2

$P < 0.001$

Note: Post hoc contrasts are described in *Results by ant species.* Individual queens were scored positively (+) if they colonized or attempted to colonize at least one of the host species within a pair and negatively (−) if they failed to colonize or to attempt to colonize both host species within a pair. The McNemar test corrects for nonindependence of tests within queens by considering only those queens that scored positively for one pair and negatively for the other (+/− or −/+ queens) (see Sokal and Rohlf 1995). Two-tailed *P* values are calculated using an exact binomial test (Engels 1988*a*). *P* values given for post hoc tests are not corrected for unplanned tests.

† M = *C. membranacea,* Pg = *C.* prov. *pugnara,* Pb = *C.* prov. *puberula,* E = *C.* cf. *engleriana;* + = colonization attempt (behaviors 4 or 3), − = failed colonization (behaviors 0, 1, 2, or 5).

TABLE 12. Summary results of the queen preference (QP) experiment.

Ant species	Behaviors†	*Cecropia* species			
		cf. *engleriana*	prov. *pungara*	*membra-nacea*	prov. *puberula*
A. ovaticeps	Colonizes plant (4)	5	5	11	9
	Unable to enter (3)	1	1	1	1
	Rejects plant (0,1,2,5)	14	14	8	10
A. australis	Colonizes plant	16	...	...	14
	Unable to enter	...	10	1	...
	Rejects plant	4	10	19	6
P. luteola	Colonizes plant	...	18		
	Unable to enter	...	...		
	Rejects plant	20	2		

† Numbers in parentheses indicate queen behaviors; see *Methods: Queen preference experiment (QP)* for an explanation of the numbered behavior categories.

cf. *engleriana,* often within less than a minute. Thus, *A. australis* was unable to enter the prostoma (behavior 3) significantly more often on *C.* prov. *pungara* than on *C. membranacea* (Table 11E). The test queens used in this study had been collected from a variety of Cecropia saplings: *C. pungara* (one), *C. polystachya* (two), *C.* cf. *engleriana* (three), and *C. puberula* (nine). We detected no effect of source plant or presentation order on the probability of colonizing (data not shown but available on request).

Pachycondyla luteola

Colonization frequencies.—Since *P. luteola* did not colonize either of the hosts represented in CE2, the data summarized here apply exclusively to CE1. With 138 colonizing queens collected from inside stem internodes, *P. luteola* was the second most common species (Table 2). Its queens were strongly and significantly overrepresented in the forest gap habitat, and the frequency of colonization was not independent of host species (Tables 2 and 8). Seventy-four percent of queens colonized *C.* prov. *pungara,* and 23% were found on *C. membranacea.* The remaining four queens occurred on *C.* prov. *puberula,* and none occupied *C.* cf. *engleriana.* A post hoc comparison revealed significantly greater representation of *P. luteola* on *C.* prov. *pungara* than on the other three species (extrinsic null hypothesis of equal distribution between *C.* prov. *pungara* vs. *C. membranacea, C.* prov. *puberula,* and *C.* cf. *engleriana,* $G_{adj} = 32.776$, df = 1, $P < 0.001$).

In addition to the queens inside stem internodes, many *P. luteola* queens were also found stationed beneath leaf laminae and on the external stems of *Cecropia* saplings. These external queens occurred only in the forest gap habitat and, in order of decreasing abundance, on *C.* prov. *pungara, C.* prov. *puberula,* and *C. membranacea.* This comparison, which roughly paralleled the distribution of colonizing queens, held for both numbers of saplings with external queens, and the number of queens per sapling. For example, summed over all blocks on 5 August, the date of the first collection, *C.* prov. *pungara* had 30 external queens, *C* prov. *puberula* 10, *C. membranacea* 7, and *C.* cf. *engleriana* none. Relative constancy over weeks in the numbers of queens per sapling suggested that individual external queens were present for long time periods.

Mortality.—Since mortality was so low (Table 2), we did not analyze the effect of habitat or plant species on mortality.

Brood production.—When broods were defined to include eggs as well as larvae and pupae, neither habitat ($G = 0.185$, df = 1, $P = 0.667$) nor host species (Table 10) significantly affected brood production by live queens. However, while neither larvae nor pupae were found in the brood of any of the 16 egg-producing queens from *C. membranacea* and *C.* prov. *puberula,* representatives of one or the other of these stages were found with 14 of the 52 egg-producing queens from *C.* prov. *pungara* (Monte Carlo, $P = 0.036 \pm 0.001$ SE, Table 10). Although this significant result suggests that *C.* prov. *pungara* may be required for brood maturation, all but one of the egg-producing queens in *C. membranacea* and *C.* prov. *puberula* had been resident for less time than the minimum residence time (37 d) of queens producing advanced brood stages in *C.* prov. *pungara.* Thus, we cannot exclude the confounding effect of time in larval production. Lower mean residence times in *C. membranacea* (16.0 ± 11.4 d; mean ± 1 SD) and *C.* prov. *puberula* (16.6 ± 11.2 d) than on *C.* prov. *pungara* (35.63 ± 22.9 d) (Kruskal-Wallis, $U = 13.69$, df = 2, $P = 0.001$) are due to a higher proportion of colonizations later in the experimental run. Finally, the failure of *P. luteola* to colonize the closely related species pair *Cecropia* sp. A and *C.* cf. *engleriana* in CE2 is consistent with the absence of this ant from *C.* cf. *engleriana* in CE1 and in nature (Tables 1 and 2).

QP experiment.—*P. luteola* queens colonized *C.* prov. *pungara* significantly more often than they colonized *C.* cf. *engleriana* (Table 11F). In addition, *P. luteola* actively rejected *C.* cf. *engleriana* in 12 of 20 cases by leaving the plant within 60 min (behaviors 1 and 2). In the only two cases in which *P. luteola* did not colonize *C.* prov. *pungara,* the queens remained on the plant for the entire hour. We detected no effect of

presentation order on the probability of colonization (data not shown). All but one of the test queens used here had been collected from wild saplings of *C. pungara.* Therefore, we cannot entirely rule out differential colonization of this host due to source plant effects, though we can rule out the possibility that *P. luteola* queens are prevented in some way from colonizing *C. engleriana* saplings (as in *A. australis* on *C. pungara* above).

Discussion

Patterns in the natural distribution of *Cecropia*-ants across habitats and host species (Table 1) are largely explicable by events occurring at the stage of host colonization by ants (Tables 2, 3, 8, and 11). Trends in queen mortality and brood production can also influence the probability that young colonies establish successfully (Tables 5, 6, 7, 8, 9, and 10). We begin by summarizing patterns of habitat-specific and host-specific colonization, and then consider whether queens selectively colonize the habitats and hosts where their colonies are likely to be most successful.

Habitat-specific colonization

Although habitat specialization by different ant species has been implicated as a factor promoting specificity in both the ant–*Cecropia* system (Benson 1985, Longino 1989*a*, Davidson and Fisher 1991) and other ant–plant symbioses (Davidson et al. 1991), evidence for host and habitat specialization by ants is often confounded due to habitat specialization by hosts. In such cases (e.g., Table 1), evolved host-specificity cannot be separated from the sorting out of ant species over plant species due to ecological factors alone (ecological species fitting or sorting, see Janzen 1985). Ours is the first attempt to disentangle host and habitat specialization experimentally, and our results represent the strongest evidence to date that habitat-specific colonization contributes significantly to specificity in the host associations of obligate plant-ants.

At least four ant species (and probably also *Azteca alfari*) showed significant habitat associations in one or both of the experiments (Table 8). Most strikingly, colonization by *Azteca ovaticeps/alfari* was almost completely restricted to the riverside habitat in both CE1 and CE2. For the most part, habitat association in these ants explains the limitation of their natural host ranges to the three pioneer *Cecropia* species (Table 1). Similarly, the preference of *P. luteola* queens for forest gap habitat is consistent with that species' specialization on *Cecropia pungara,* though host-specificity is also important in this species. Within habitats, host species were sampled evenly in colonization experiments but not in our preliminary survey of established colonies (Table 1). Therefore, it is not appropriate to test whether relative colonization in riverside and gap habitats (Tables 2 and 3) matches the habitat distribution of established colonies (Table 1). However, consistent with the distribution of established colonies, both *A. australis* and *Camponotus balzani* colonize saplings in both habitats, though *Camponotus balzani* may predominate more as colonists than as colonies in gap habitat. If the latter disparity is real, it would suggest that some postcolonization process (e.g., inadequate defense against herbivores in relatively slow-growing plants of gap habitats) might limit colony establishment differentially in gap habitat. (See Davidson and Fisher 1991 for examples of other possible postcolonization processes.)

Surprisingly, the habitat affiliations of *Azteca australis* differed between CE1 (overrepresentation in riverside habitat) and CE2 (overrepresentation in forest gap habitat). We contend that these results are mediated by proximity to foundress sources (cf. Vasconcelos 1993), rather than by alternating habitat specialization. At our research site, the most common *Cecropia* species in lowland forest are *C. membranacea,* along the river margin, and *C.* prov. *pungara* in forest gaps. Because *A. australis* tends to discriminate against these hosts (Tables 1, 2, 8, 11, and 12), the nearest sources of *A. australis* queens for our lowland experimental plots (CE1) were primarily upland populations (across the river) of both forest gap species (*Cecropia* sp. A and *C. ficifolia*) and riverside species (*C.* cf. *engleriana* and *C. polystachya*). Since these queen sources lay closer to riverside plots than to forest gap plots on the opposite (lowland) bank (Fig. 2), the riverside plots could have received more *A. australis* foundresses (Table 2) due to proximity alone. Similarly, the significant block effects for colonization of the CE1 forest gap plots by *A. australis* may have been due to patchy colonization from these distant propagule sources.

In contrast, CE2 forest gap plots were located on the upland side of the Tambopata River, close to sources of *A. australis* queens. The greater proximity of forest gap plots to queen sources in CE2 than in CE1 led to much higher levels of colonization (171 vs. 51 queens in forest gap plots) and appears also to have produced significant overrepresentation of *A. australis* in the forest gap habitat (Tables 3 and 8). Riverside plots on the upland (CE2) and lowland (CE1) banks experienced comparable colonization in the two experiments (109 and 100 queens, respectively, Tables 2 and 3). In summary then, *A. australis* frequently colonized both riverside and gap habitats, and the degree to which it predominated in one or the other habitat depended strongly on proximity to propagule sources.

Despite this (admittedly retrospective) evidence that proximity to natural foundress sources can influence colonization rates in *A. australis,* it seems unlikely that sources of foundresses account for the habitat associations of the other ants, whose habitat affiliations did not differ between experiments. Hosts acceptable to *Camponotus balzani* queens occur naturally in both uplands (*C. membranacea* and *C. ficifolia*) and lowlands (*C. membranacea* and *C.* prov. *pungara*), and the same

TABLE 13. Percentages of total colonizing queens (live and dead; Tables 2 and 3) and established colonies (in parentheses, from Table 1) across host species. *P* values comparing the two sets of percentages were calculated using Monte Carlo contingency table tests. Frequencies of colonizing queens across host species are either marginally or not significantly different from frequencies of established colonies in all but two cases. Queens of *Azteca ovaticeps* are less abundant on *C.* cf. *engleriana* than are colonies, and queens of *Camponotus balzani* are present on *C.* cf. *engleriana* (CE2), *C.* sp. A (CE2), and *C. puberula* (CE1) saplings (indicated by parentheses) but are absent in mature trees.

Experiment	*Cecropia* species	Ant species				*P*
		Camponotus balzani	*Azteca ovaticeps/alfari*	*Azteca australis*	*Pachycondyla luteola*	
CE1	*membranacea*†	12 (30)	58 (49)	21 (21)	9 (0)	0.055
	cf. *engleriana*†	0 (0)	25 (83)	75 (17)	0 (0)	0.008
	pungara‡	8 (10)	0 (0)	0 (0)	92 (90)	1.000
	puberula‡	13 (0)	0 (0)	77 (100)	10 (0)	0.046
CE2	cf. *engleriana*†	9 (0)	43 (83)	48 (17)	0 (0)	0.100
	sp. A‡	35 (0)	0 (0)	65 (100)	0 (0)	0.002

† Colonization frequencies taken from the forest gap habitat only.
‡ Colonization frequencies taken from the riverside habitat only.

can be said for *Azteca ovaticeps/alfari* (*C. membranacea* and *C.* cf. *engleriana* on both lowland and upland riverbanks, and *C. polystachya* on upland riverbanks) (Tables 1–3; see also Davidson and Fisher 1991). Plots in both habitats lay within easy reach of foundress sources for these two ant species. Similarly, several sources of *P. luteola* queens (mature trees of *Cecropia* prov. *pungara* in forest gaps) lay within tens of meters of the riverside habitat, and at least as close to riverside plots as to forest gap plots. We conclude that foundresses of *A. ovaticeps/alfari, C. balzani,* and *P. luteola* have evolved habitat-restricted searching behavior either before, coincidentally with, or after becoming obligately associated with *Cecropia.*

Host-specific colonization

Independently of habitat associations, significant host plant specificity was detected in each of the focal ant species. Riverside specialists *Azteca ovaticeps/alfari* were overrepresented on two pioneer species, *C. membranacea* and *C.* cf. *engleriana,* in CE1 (Tables 2 and 8), and on the latter host in CE2 (Tables 3 and 8). However, the QP experiment revealed no significant host preference by *A. ovaticeps* queens (Table 11A and B), even though the ranking of host acceptance was similar to that of colonization frequencies by host species in CE1.

The discrepancy between the nonsignificant results of the QP experiment, and the significant results of colonization experiments is intriguing. One possible explanation is that queens discriminate among hosts using cues that are effective from a distance but not in situ (e.g., Ware and Compton [1992], for fig wasps). Alternatively, the ability of *A. ovaticeps/alfari* queens to discriminate among hosts may be so weak (in contrast to the results with *A. australis* and *P. luteola*) that it was easily confounded by the placement of queens on a variety of hosts in the QP experiment. Our use of deälate queens could also have biased the QP experiments against detection of host preferences in weakly discriminating ant species, since with wings removed, queens had very limited opportunities for reaching other host plants. If host discrimination is comparatively weak in *A. ovaticeps/alfari,* then overrepresentation of these ants on the pioneer host species typical of riverside environment might simply have been due to queen orientation to familiar cues presented by natal host plants (cf. Turlings et al. 1993 for parasitoid wasps).

In the three remaining species, explanations for host-plant associations may be more straightforward. *Camponotus balzani* exhibited no detectable plant species affiliations in CE1 (Tables 2 and 8), though it was significantly associated with *Cecropia* cf. *engleriana* in CE2 (Tables 6 and 8). The simplest interpretation of its lower frequency on *Cecropia* sp. A is that many of the internodes of this host are too small to accommodate the relatively large *Camponotus* queens (Davidson and Fisher 1991). In contrast, for *Azteca australis* and *Pachycondyla luteola,* results of the QP experiments (statistically significant in each case, Tables 11 and 12) were strongly consistent with the differential colonization of particular host species in the colonization experiments. With the notable exception of *A. australis* on *C.* prov. *pungara,* queens of these species did not attempt to enter stems of the less frequently colonized host species. The behaviors of queens in these two species suggest evolved host-specificity.

Table 13 compares queen colonization frequencies to the relative abundances of established colonies (from Table 1). Several shortcomings of the data on established colonies are likely to preclude a good match. That is, data in Table 1 represent a composite survey of three sites, none of them overlapping with our experimental site, and the relative abundances of ant propagules almost certainly differ from those at our site.

Second, some sample sizes (most notably that of *C.* cf. *engleriana*) are inadequate to accurately characterize the relative frequencies of different ant associates. Despite these problems, a very stringent test of the match between colony and colonization frequencies provides strong evidence contradicting the match in only two cases. (Two marginally significant differences are mainly or partly due to the failure of *P. luteola* to establish colonies on all but its preferred host. This finding was confirmed in our colonization experiments.) First, *Cecropia* cf. *engleriana* was colonized less frequently by *A. ovaticeps* than by *Azteca australis,* the reverse of the pattern for established colonies. This discrepancy, significant in CE1 but not CE2, could simply reflect a difference in propagule availability; *C. membranacea,* an important source of *A. ovaticeps* propagules, is much less common at our experimental sites than at sites where established colonies were censused. Second, queens of *C. balzani* colonized saplings of *C.* cf. *engleriana, C. puberula* and *C.* sp. A, but established colonies have not been found in these host species. Absence of established colonies from *C.* cf. *engleriana* might have resulted from inadequate sampling of this host (Table 1), as evidenced by the nonsignificant *P* value in CE2 (Table 13). Since exhaustive sampling of naturally occurring *C.* sp. A seedlings (Davidson and Fisher 1991) and more modest sampling of *C. puberula* (D. W. Yu and D. W. Davidson, *unpublished data*) failed to turn up any queens of *C. balzani* in other studies, one might speculate that high postcolonization mortality, acting over longer time scales than studied in our experiments, may limit host breadth in *C. balzani.* It is also possible naturally occurring *C.* sp. A seedlings have smaller internodes on average than those of our cultivated seedlings in CE2.

Queen success in typical vs. atypical habitats and hosts

Are queens most successful in the habitats and host species most frequently colonized in our experiments? Rates of queen mortality, parasitoid attack of queens, and brood production provide three estimates (albeit not independent ones) of queen success.

We detected no effect of host species on ratios of live to dead queens, but in the two ant species for which habitat effects on queen mortality could be tested (*A. australis* and *C. balzani*), mortality was significantly higher in the riverside habitat (CE1 and CE2, Tables 2, 3, and 8). In large part, parasitoid wasps may account for the high mortality in *Azteca ovaticeps/alfari, A. australis,* and *Camponotus balzani* queens in the riverside plots. We scored mortality from parasitoids only if a larval, pupal, or adult wasp was found in the same internode, although in the riverside habitat, we found many other dead queens with the hollow exoskeletons possibly indicative of parasitoid attack. Our conservative scoring method almost certainly underestimates the total mortality from parasitoids, but it clearly demonstrates that parasitoid pressure is much higher in the riverside habitat than in forest gaps (Table 5). The highly significant association of parasitoids with the linear and continuous riverside habitat, where *Cecropia* (mainly *C. membranacea*) occurs in almost continuous stands, is consistent with recently published evidence that parasitoid wasps are less likely to disperse to habitat fragments (Kreuss and Tscharntke [1994], see also McDade and Kinsman [1980] for an example with parasites of pollination mutualisms), such as the patchily distributed forest light gaps in this study.

Although brood production by *Cecropia*-ants was apparently not influenced by habitat type, it did vary significantly with host species in one and possibly two cases. First, *Azteca australis* produced brood only in *C.* prov. *puberula* and *C.* cf. *engleriana* (Table 10), the two hosts which it colonized disproportionately (Tables 2, 3, and 8). Second, although the failure of *P. luteola* to produce larvae and pupae on colonized hosts other than *C.* prov. *pungara* might well have been due to later colonizations leading to lower mean residence times on those hosts, the later (and fewer) colonizations are themselves strongly suggestive that *P. luteola* queens may have been colonizing *C. membranacea* and *C.* prov. *puberula* only after the *C. pungara* saplings became saturated with colonizing queens. In a prior field experiment (D. Davidson and P. Herrera, *unpublished data*) in which *P. luteola* queens were placed on both *C.* prov. *pungara* and *C. membranacea,* the majority of queens remained on *C.* prov. *pungara* for the entirety of the 6-wk experiment, but most of those on *C. membranacea* vanished in just a few days. Contrasted with the relatively small and soft Müllerian bodies of the latter host (Folgarait and Davidson 1994, 1995), the uniquely large and hard bodies of *C.* prov. *pungara* may be essential for brood production and the maintenance of queen activities in *P. luteola,* and perhaps more resistant to decay during storage.

To summarize, habitat- and host-specific colonization may enhance queen survivorship and brood production in certain cases. Queen mortality was strongly related to habitat type in the two ant species tested, but *Camponotus balzani* was unique in colonizing at higher rates in the habitat with lower queen mortality. Nevertheless, postcolonization processes might later reduce survivorship in that same habitat (Table 1). Some evidence also suggests that the two most host-specific ant species (*A. australis* and *P. luteola*) are overrepresented as colonists on the hosts where brood production is most successful. If these effects are real, they would reinforce rather than weaken the patterns of species-specificity established during colonization. Below, we examine some possible historical explanations for the patterns of colonization noted in our experiments.

Multiple modes of origin in Cecropia*-ants*

Among the five ant species studied here, obligate dependency on *Cecropia* has arisen at least four times

independently (see *Introduction*). Only *Azteca ovaticeps* and *A. alfari* appear to share a relatively recent common ancestor specialized to *Cecropia* (see Longino 1989*b*, 1991*a* and Ayala et al. 1996). The evolutionary route to symbiosis need not have been identical in each case, and our data suggest that it was not.

Habitat specialists and host generalists.—At least *Azteca ovaticeps* and *Camponotus balzani* (and perhaps *A. alfari,* see Harada and Benson 1988), exhibited strong habitat-specificity and weak host affiliations during colonization (see *Queen success in typical vs. a typical habitats and hosts*). Host choice in the former species might be entirely explicable by queen orientation to natal hosts, and that of the latter species may emerge only from the inadequate internode sizes of *Cecropia* sp. A. With host discrimination so limited, it is perhaps likely that specialization to habitats has preceded the evolution of host-specificity, and possibly even the origins of symbiosis with *Cecropia.* To further consider the evidence for this hypothesis, we look first at the phylogenetic affinities of *A. ovaticeps/alfari*; nothing is currently known about the affiliations of *C. balzani.*

Based on morphological and behavioral data, Longino (1989*b*) argued that the affinities of *Azteca* ants in the "*alfari* group" lie with other *Azteca* that occupy live stems of a diversity of plants (e.g., *Cordia alliodora* Cham., Boraginaceae) with or without preformed cavities. These ants tend Homoptera in cavities that they or other stem-boring insects have excavated in live plant stems. As do *A. ovaticeps* and *A. alfari* on *Cecropia* (Longino 1991*a*), colonies of these other stem-nesters abandon older stems to maintain polydomous nests in newer and more productive growing tips. Thus, prior to the movement of *A. ovaticeps* and *A. alfari* onto *Cecropia,* their nesting habits, or the habits of a putative common ancestor, may have been much as they are today. They may have nested in some other myrmecophyte, or in hollow live stems of any of a number of second-growth tree species. Such trees are selected for fast growth and large leaf surface areas with minimal support structure, and they are often sparsely branched, with thick, pithy stems (White 1983) that both attract stem-boring insects and provide nesting opportunities for ants (Davidson and McKey 1993). Our occasional observations of *A. ovaticeps/alfari* queens attempting to enter *C. membranacea* stems and trichilia prior to stem swelling (D. W. Yu and D. W. Davidson, *personal observation*) are consistent with the hypothesis that a recent ancestor of these ants could have nested in a variety of tree species whose stems lacked prostomata. A recently completed molecular phylogeny of the *Azteca* supports the scenario given here by identifying *A. ovaticeps* and *A. alfari* as sister species and placing this pair closest to *A. patruella,* a nonmyrmecophytic, stem-dwelling ant (Ayala et al. 1996).

A morphological trait of these stem-nesting *Azteca* may limit the dispersal of *A. ovaticeps* and *A. alfari* away from riverine edges. Queens of both species have weakly developed thorax muscle masses in comparison to queens of congeneric *Cecropia*-ants (Davidson and Fisher 1991). Although the resultant, more streamlined body outline of the former two species may facilitate entry into small stem openings, it could also compromise the ability to search for isolated hosts in forest gaps. Search times may be lower in continuous and linear riverside edge, where *Cecropia* are abundant.

Several anecdotal observations suggest that *Camponotus balzani* may be a recent and secondary associate, and perhaps a parasite, of relationships between *Cecropia* and other ants. *C. balzani* is unique in several ways among the obligate *Cecropia*-ants studied here. First, queens do not discriminate against hosts and habitats where success in colony founding may be relatively low (Table 1). Second, their principally nocturnal activity schedules leave plant parts unattended in the daytime, and vulnerable to herbivores, such as Chrysomelid beetles. Third, workers are minimally active on leaf laminae, and unlike the other *Cecropia* ants, they do not attack chemically defended chrysomelid larvae (D. Davidson and P. Herrera, *unpublished data*). Finally, *C. balzani* workers are alone among the five focal ant species studied here in recognizing baits of tuna or cheese as food (Davidson and Fisher 1991); their diets appear to be less specialized to food rewards provided by their hosts. If these ants make greater use of other food sources (e.g., Homoptera), this may help to explain their ability to persist on a wide range of hosts that differ in the quality and quantity of food provided to ants (Folgarait and Davidson 1994, 1995, and see below).

If *A. ovaticeps/alfari* and *Camponotus balzani* are indeed recent and secondary associates of *Cecropia,* these ants may simply not have had an opportunity to evolve strong host specificity (or in the case of *C. balzani,* new and selectively advantageous habitat associations). Other explanations are possible, however, and the evolution of host generalists from specialists may not be uncommon (reviewed in Thompson 1994).

Azteca australis*: a host specialist and habitat generalist.*—Ants that do not depend on live, preformed, or modifiable plant cavities can presumably place their nests anywhere. Many such ants (e.g., those nesting in carton or rolled leaves, and including *Azteca* species with large and exposed carton nests) place their nests on host plants that provide some form of food reward, usually in the form of extrafloral nectar (see, e.g., Davidson and Epstein 1989). In order for such species to take maximum advantage of their ability to position nests near food, selection should have favored both mechanisms for host-plant recognition and the capacity for sustained flight during the search for unoccupied hosts. Both of these attributes are combined in *Azteca australis* queens, which possess a well-developed thorax and wing musculature.

This combination of traits may be understandable in the context of Longino's (1989*b*, 1991*a*) assessment that the affinities of this species lie with a group of *Cecropia*-specialists in the *Azteca xanthochroa* complex (Longino 1991*b*). These ants concentrate their queen, all brood, all cached Müllerian bodies and many sexuals in a centralized and large carton nest located in a small number (≈ 2) of internodes in the approximate center of the tree. Longino interprets this nest structure as relictual evidence of an evolutionary past in which the ants lived in large and exposed carton nests. Based on the results of our own study, we suggest that the ancestors of *A. australis* could have specialized principally on hosts, rather than habitats, because even before they evolved the habit of living in host plant stems, they sought out *Cecropia* for its food rewards. Since the probable sister group of *Cecropia* (African *Musanga,* which have only opportunistic associations with nonresident ants [Janzen and McKey 1977, Berg 1978]) also produces pearl bodies (D. W. Davidson, *personal observation* of cultivated plants), pearl body production may have predated true myrmecophytism in *Cecropia* and have provided a substantial attractant to carton-nesting ants with relatively unspecialized diets. Similarly, based on comparisons among myrmecophytic and nonmyrmecophytic species, Fiala and Maschwitz (1991, 1992*a*,*b*) have argued that food body production preceded myrmecophytism in *Macaranga* (Euphorbiaceae), the ecological equivalent of *Cecropia* in Asian rain forests.

Why should *A. australis* show such strong host preferences? Although all well-studied myrmecophytic *Cecropia* species produce the same two food rewards, Müllerian and pearl bodies, both the amounts and proportions of the two types of food rewards differ among species (Folgarait and Davidson 1994, 1995). Moreover, the constituents of the two rewards differ substantially, with Müllerian bodies consisting mainly of carbohydrate (glycogen surrounded in proteinaceous membranes, Rickson 1976), and pearl bodies containing both carbohydrate (lipids, Rickson 1976) and amino acids (Folgarait 1993, see also Folgarait and Davidson 1994, 1995).

In *A. australis,* as in ants generally, colony growth may be limited principally by the availability of protein (e.g., Markin 1970, Davidson and Patrell-Kim, *in press*). Upon comparison of our results with data from the Folgarait and Davidson studies, we find that *A. australis* appears to do well on hosts (*C.* cf. *engleriana* and *Cecropia* sp. A [Tables 1, 9, and 10]) that produce a wealth of pearl bodies, and to avoid hosts (e.g., *C. membranacea* and *C.* prov. *pungara*) where pearl body production is limited, perhaps as a consequence of adaptation by these plants to frequently inundated habitats with nitrogen-poor soils (D. W. Davidson and D. W. Yu, *unpublished data*). Pearl body production has not yet been studied in *C.* prov. *puberula.* If the overrepresentation of *A. australis* on *C.* cf. *engleriana* in CE2 is indicative of a preference for this host over *Cecropia* sp. A (not included in the QP experiments), such a preference might be based on the larger leaf areas and intrinsically higher leaf production rates of the former species (Folgarait and Davidson 1994, 1995); both attributes translate into higher rates of production of ant rewards. Moreover, within pairs of close relatives, pioneers (e.g., *C.* cf. *engleriana*) exceed gap species (*Cecropia* sp. A) in pearl body production per unit leaf area (though the reverse is true for Müllerian bodies, Folgarait and Davidson 1994, 1995). Finally, hosts with comparatively low pearl body production might be more available to *A. ovaticeps/alfari* than to *A. australis* if nitrogen demand is lower in the former species, which have smaller colonies that occupy just the growing tips of host plants rather than the entire host tree, as in *A. australis* (see Longino 1991*a*).

The statistically significant effect of host species on brood production in CE1 may be due to the fact that the *C.* cf. *engleriana* and *C.* prov. *puberula* saplings used in this experiment developed much thicker parenchymal layers than did the saplings of *C. membranacea* and C. prov. *pungara* (D. Yu, *personal observation*). Parenchymal layers contain water and perhaps also nutrients that may help maintain foundresses and/or contribute resources for brood production. In colonized internodes, these layers are often scraped away from stem walls, and their dried remnants accumulate in waste heaps. Any effect of host species on brood production is apparently a weak one, since *A. australis* sometimes establishes on *C. membranacea,* which has a thin parenchymal layer (Table 1).

Pachycondyla luteola*: a host and habitat specialist.*—Like *A. australis, P. luteola* is a host specialist, but host specialization is more extreme in this case. The only other hosts colonized by foundresses of this ant species are *C. membranacea,* the probable sister species of the typical host, and *C.* prov. *puberula,* which hybridizes with the principal host (see *Introduction*). In the colonization and QP experiments, *P. luteola* queens avoided colonizing members of the more distantly related species group consisting of *C.* cf. *engleriana* and *C.* sp. A. Not surprisingly, given the extreme host specialization of *P. luteola,* this species colonized disproportionately in forest gaps, the characteristic habitat of *C.* prov. *pungara.*

How might the uncharacteristically species-specific relationship between *P. luteola* and *C.* prov. *pungara* have arisen? We conclude that this is a case of pairwise coadaptation, a relative rarity in ant–plant symbioses (Davidson and McKey 1993). Although the precise phylogenetic affiliations of *P. luteola* are unknown (W. L. Brown, *personal communication*), the species is apparently not closely related to congeneric *Cecropia*-ants (*Pachycondyla* species nr. *villosa,* nr. *unidentata,* nr. *bugabensis,* and prov. *dianae*). It is therefore unlikely to have shared a *Cecropia*-specialized common ancestor with any of these other four species. Virtually

unique within the genus, as well as among the four best-studied *Pachycondyla* species (excluding nr. *bugabensis*) obligately associated with *Cecropia, P. luteola* has numerous derived traits (Davidson and Fisher 1991, Verhaagh 1994, and this study), including: (1) worker fidelity to host-plants during foraging, (2) huge colony sizes, with tens or hundreds of thousands of workers on a single 30–35 m tree, (3) an unusually pronounced worker-queen size dimorphism, and (4) extremely aggressive workers with formidable stings, producing painful wounds that may serve as long-term reminders to potential vertebrate aggressors to avoid *Cecropia* prov. *pungara* (see also McKey 1974).

Cecropia prov. *pungara,* the principal host of *P. luteola,* also has a number of derived traits. In phylogenetic analyses of morphological and molecular sequence data on 12 *Cecropia* species (D. Davidson, *unpublished data* including all species but *puberula* from this study), probable sister species *C.* prov. *pungara* and *C. membranacea* formed the best supported clade. In each case, the former species had the greater number of derived traits, though by just one base pair in the analyses of ITS 1 and ITS 2 nuclear ribosomal sequences. Several derived morphological traits could have evolved under selection pressures imposed by *P. luteola.* Such traits include the unusually large prostoma and Müllerian bodies (possible responses to especially large queen and worker body sizes), and earlier developmental onset of myrmecophytism (Davidson and Fisher 1991). Furthermore, in the QP experiments, some attribute of the prostoma of *C.* prov. *pungara* appears to preclude its discovery and use by *A. australis* queens. Such a trait could have evolved as an exclusion filter (sensu Thompson and Pellmyr 1992), who have argued that such barriers are prerequisites for strict, pairwise coevolution in other types of mutualism. Alternatively, exclusion of *A. australis* may be an accidental consequence of coadaptation of this host with *P. luteola.*

Evolutionary specialization in *P. luteola* and *C.* prov. *pungara,* and the acquisition of matching or correlated traits, probably have resulted from a combination of mutual preadaption and coadaptation. A common ancestor of sister species *C. membranacea* and *C.* prov. *pungara* could have been distinctive in ways favoring association with *P. luteola.* The stem pubescence of these species is longer, sparser, and more suitable for supporting movement of large-bodied ants than is the very short pubescence of most other *Cecropia.* Among 11 myrmecophytic *Cecropia* surveyed to date in common garden experiments, these sister species also have the largest (*pungara*) and second largest (*membranacea*) prostomata and Müllerian bodies, and are unique in producing trichilia (and therefore Müllerian bodies) before stems expand and prostomata appear (Folgarait and Davidson 1994, 1995; S. Adondakis, *unpublished data*). Production of Müllerian bodies early in sapling development may have constituted a felicitous match to the need for *P. luteola* queens to forage during early colony establishment. Unlike *Azteca* and *Camponotus* queens, which found their colonies claustrally (relying on internal resources such as histolyzed wing muscle as resources for the first brood), *P. luteola* queens require external food resources. Nonclaustral colony founding is typical of the subfamily Ponerinae, to which *Pachycondyla* ants belong. Claustral founding may be a superior strategy for avoiding predation and parasitism (Hölldobler and Wilson 1990), and perilampid wasps (Chalcidoidea) do parasitize *P. luteola* brood through the open prostomata left by foraging *P. luteola* queens in saplings of *C.* prov. *pungara* (Davidson and Fisher 1991). Nevertheless, early production of Müllerian bodies by a putative ancestor of *C. prov. pungara* and *C. membranacea* could have enabled the ancestor of *P. luteola* to harvest and eat or store these food bodies in lower stems or beneath the stipules of newest leaves (D. W. Yu and D. W. Davidson, *personal observations*). The availability of Müllerian bodies as resources for the first worker brood may accelerate colony establishment in *P. luteola,* and favor this species over potentially competing claustral species such as *Camponotus balzani.* Nonclaustral founding in *P. luteola,* and the early production of Müllerian bodies in *C.* prov. *pungara,* appear to us to be an example of mutual preadaption setting the stage for further, coevolved specificity.

Ecological fitting vs. evolutionary specialization

The diversity of mechanisms underlying species-specificity in *Cecropia*–ant relationships may be a direct consequence of the independent (or horizontal) dispersal of symbionts. Seeds of myrmecophytes disperse separately from ant associates, and ants colonize host plants only after sapling establishment. Typically, the predominance of horizontal transfer of symbionts over vertical transmission inhibits pairwise coevolution and co-cladogenesis (Thompson 1994). Therefore, it is not surprising that much of the species diversity of ant-plants and plant-ants worldwide appears to be due to repeated evolutionary colonization of partners by preadapted lineages, rather than to co-radiation of congruent lineages (Davidson and McKey 1993).

Nevertheless, historical coincidences (e.g., preadapted habitat affiliations of hosts and ants, or preadapted capacities for host discrimination by ants) appear to have determined the initial pairings of ants and *Cecropia* in ways that affected subsequent opportunities for diffuse or pairwise coevolution (cf. Janzen 1985). Although horizontal transfer is often interpreted as uniting symbionts at random, this appears not to have been the case in relationships between *Cecropia* and its ants. Here, a combination of coordinated dispersal and exclusionary dispersal (to the same or different habitats, respectively) appears to have been key to the pairing of symbionts. Moreover, the resultant pattern of ecological fitting is not an alternative to pair-

wise or guild coevolution, but rather sets the stage for future coevolution of one type or another. A challenge for coevolutionary studies is to determine whether traits that result in coordinated dispersal are a general and ancestral feature of associations thought to be strongly coadapted.

The niche partitioning that results from ecological fitting (Table 1) appears to be derived more from the historical coincidences described above than from selection to avoid competition for hosts. The role of niche diversification in response to competition might be expected to increase through time, as *Cecropia* accumulates more ant partners.

Interaction structure over space and time

Ecological studies at a single site provide, at best, indications of the factors affecting specialization over space and time (see, e.g., Thompson 1994). The evolution and ecology of the plant-ants studied here may well have been shaped by selective forces operating elsewhere in the present and past distributions of these ants. Here we consider the evidence for geographic variation in the composition and structure of *Cecropia*–ant interactions.

Most literature reports on *Cecropia*–ant relationships refer to ecological guilds of obligate *Cecropia*-ants interacting with taxonomic guilds of these myrmecophytic trees (Benson 1985, Harada and Benson 1988, Longino 1989*a*, *b*, 1991*a*, *b*). Despite variation in the species composition of these relationships, the interaction structure appears to be relatively constant. Both *Cecropia* guilds and ant guilds regularly include species specializing on different-sized disturbances (Benson 1985, Harada and Benson 1988, Longino 1989*a*, 1991*a*, *b*, Davidson and Fisher 1991), and key features of our *Cecropia*-ants are preserved elsewhere in the geographic ranges of these ants. First, for *Pachycondyla luteola,* known only from western Amazonian Peru (Departments of Madre de Dios, Ucayali, and Loreto), established colonies have been reported only from *Cecropia* prov. *pungara,* which is typical of forest gaps and swamp edges throughout its range (Verhaagh 1994; D. Davidson, *unpublished data*). Second, both species of the *Azteca alfari* group (*alfari* and *ovaticeps,* Longino 1989*b*) have been noted as characteristic of second-growth habitats (rather than the forest interior) throughout their full distributional ranges from Mexico to Argentina (Benson 1985, Harada and Benson 1988, Longino 1991*b*), and have been collected from several *Cecropia* species within single sites (Harada and Benson 1988). Third, though both the ecology and distribution of *Camponotus balzani* remain poorly characterized, *C. balzani* is a common associate of *Cecropia ficifolia,* a forest gap species at Jatun Sacha Biological Station, Ecuador (see Table 1, D. W. Yu, *personal observation*).

Fourth, although limited data and taxonomic uncertainties preclude confident generalizations about the habitat affiliations of *Azteca australis,* the available evidence suggests that habitat associations in Peru are typical for the species. Harada and Benson (1988) list *Azteca* sp. indet. as occurring in both forest gaps and large clearings. They note that this species is morphologically similar to *Azteca xanthochroa,* an ant restricted to Central America but considered closely allied to *A. australis.* Based on a recent taxonomic revision of all the *Cecropia*-inhabiting *Azteca* (Longino 1991*b*), *A.* sp. indet. could be one of only two *Azteca* species, *muelleri* and *australis.* Since Harada and Benson explicitly identify *A. muelleri* in their article, it seems likely that the undetermined ant is in fact *A. australis,* and therefore that the habitat affiliations of this ant are similar in Brazil and Peru. This is so despite differences in the species composition of the *Cecropia* floras between the Brazilian and Peruvian sites. Unfortunately, patterns of host specialization in relation to pearl body production cannot be ascertained from the Brazilian data.

In summary, although there is certainly room for additional study, existing data from other sites are consistent with our experimental results and do not elicit concern for our having missed critical elements of the evolutionary ecology of the interactions by studying them experimentally at a single site. In species and sites other than those studied here, historical coincidences may have determined the basic framework of *Cecropia*–ant interactions in much the same way as we suggest for our Peruvian study system.

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Voucher collections for our *Cecropia* species are located in the herbarium of the Marshall Field Museum (Chicago), under Robin Foster's collecting numbers (with names from herbarium sheets if different from our names): *C. membranacea*—D. Davidson "sin numero" = R. Foster and B. d'Achille 12169 and 12202; *C.* prov. *pungara*—11292 ("bosque"); *C.* prov. *engleriana*—11528 (*C. engleriana* Snethlage); *C.* sp. A—12141, 12142 (*C.* aff. *engleriana*); *C. puberula*—11291; *C. polystachya* Trecul—11526.

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